FOOD OF BLACK FLY LARVAE (DIPTERA: SIMULIIDAE): SEASONAL CHANGES IN GUT CONTENTS AND SUSPENDED MATERIAL AT SEVERAL SITES IN A SINGLE WATERSHED[1]

DANIEL C. KURTAK[2]
Department of Entomology
Cornell University
Ithaca, New York 148353
U.S.A.

Quaestiones Entomologicae
15: 357-374 1979

Gut contents of black fly larvae and suspended material in water flowing over them in their stream habitats were studied for three years at five sites in a watershed near Ithaca, New York, U.S.A.

Suspended material was removed from water samples with a centrifuge. Total dry weight varied from 1–13 mg/l. Organic content (determined by dichromate oxidation) of suspended material varied from 8–24% of the dry weight. A portion of suspended material was analyzed microscopically. Particles were classified as diatoms and other algae, mineral fragments (silt), plant fragments, or fine material (<5 μm).

Quantity and quality of suspended material varied greatly at different sites in the watershed and with season. Headwater streams, especially in forested areas, contained larger amounts of plant fragments. In lower reaches there was more total suspended material and a larger proportion of diatoms. When stream discharges were low and steady, and sunshine was abundant, more diatoms were produced, while spring floods added more silt.

Gut contents of larvae were also analyzed microscopically, and the proportions of their constituents were found to agree generally with the proportions in the water. This indicated indiscriminate feeding. Also there was evidence that habitat preference had an influence on larval food. Diatoms often made up as much as 50% of some gut contents and were shown to be digested.

Le contenu du tube digestif de larves de mouche noire et le matériel en suspension dans l'eau recueillie autour des larves dans leurs habitats d'eau courante ont été étudiés pendant trois ans à cinq emplacements situés dans une zone de partage des eaux près d'Ithaca, dans l'état de New York (Etats-Unis).

Le matériel en suspension a été extrait des échantillons d'eau par centrifugation. Le poids sec total varie de 1 à 13 mg/l. La fraction organique (déterminée par oxydation au dichromate) du matériel en suspension constitue de 8 a 24% du poids sec. Une partie du matériel en suspension a été analysée au microscope. Les particules ont été classifiées soit comme diatomées et autres algues, fragments minéraux (argile), fragments végétaux, ou comme matériaux fins (<5 μm).

La quantité et la qualité du matériel en suspension varient beaucoup suivant les différents emplacements dans la zone de partage des eaux et suivant les saisons. Les ruisseaux de tête de cours, particulièrement dans les zones forestières, contiennent de grandes quantités de fragments végétaux. Dans les zones basses du bassin hydrographique, le matériel en suspension est plus abondant et la proportion de diatomées, plus élevée. Dans les cours d'eau abondamment ensoleillés et à écoulement lent et régulier, les diatomées sont produites en plus grands nombres, tandis les inondations printanières causent un apport accru d'argile.

Le contenu du tube digestif des larves a également été analysé au microscope. Les proportions des constituants présents sont généralement semblables à celles trouvées dans l'eau, indiquant que les larves s'alimentent au hasard. Il semble aussi que le choix de l'habitat ait une influence sur la nourriture des larves. Souvent, les diatomées constituent jusqu'a 50% du contenu de certains tubes digestifs et l'analyse montre qu'elles sont digérées.

---

[1]Part of a thesis accepted by the Graduate Faculty of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2]Present address: Rt. 2 Box 74R, Bishop, California 93514 U.S.A.

INTRODUCTION

Black fly larvae are filter feeders in practically all types of lotic waters, ranging from tiny streamlets to large rivers. Larvae of some species can filter material down to colloidal size (Wotton, 1976), whereas others "graze" on filamentous algae (Burton, 1973). On the basis of gut analyses, larvae feed rather indiscriminately on particulate material as shown by the studies of Anderson and Dicke (1960), Carlsson *et al.*, (1977), Chance (1970), Davies and Syme (1958), Emery (1913), Naumann (1925), Pacaud (1942), Puri (1925), Williams (1961), and Wotton (1977).

This study was designed to measure seasonal changes in the quantity and quality of suspended material at various points along the length of a stream in Tompkins County, New York, U.S.A. The gut contents of black fly larvae at each site were also examined to determine the degree of selectivity and extent to which habitat specificity influenced type of food material ingested.

MATERIALS AND METHODS

The study area

Pinkovsky (1970) and Naumann (1965) give a good ecological background for the area in central New York State (U.S.A.) where the work was done. Situated at the northern edge of the Appalachian Plateau, the area is characterized by rolling hills to the south and plains to the north. Natural vegetation is beech-maple woodland. Such vegetation exists in the more rugged areas, and on poorer soils. About 40% of Tompkins County is cultivated.

Variations in topography and vegetation produce a wide variety of stream habitats. Temperature, flow regime, discharge, substrate, and type of watershed all vary widely.

The climate is continental humid and there are large seasonal variations in stream temperature and flow. In summer months small streams dry up and large streams have low, steady, base flows. Occasionally a thunderstorm produces a freshet. In fall, winter, and spring, streams have higher and less regular flows. Snowmelt produces spring floods, with peak discharges 20–40 times the base flow (United States Geological Survey, Water Resources Data, 1965). Maximum daily water temperatures vary throughout the year and from 0 C to over 26 C for an unshaded, slow-moving stream in summer. Ice may be present for 2–3 months. Intradiel variations in temperature may be high in the summer, exceeding 10 C. There are more than 20 species of black flies present in the county (Pinkovsky, 1970, p. 156).

The sites were located along Sixmile Creek and its tributaries in Tompkins County, New York. This stream is 33 km long and originates in the uplands east of Ithaca, New York at an elevation of 520 m (Fig. 1). Flowing first for approximately 5 km through mixed wood and farm land, it then passes through a gorge and over a waterfall before travelling through 7 km of farm land and a second gorge. From there it traverses a series of waterfalls, dams and reservoirs before emptying into Cayuga Lake (elevation 117 m) at Ithaca.

Sampling sites and times

The stream was sampled at Sites 1–4 (Fig. 1), chosen as representatives of different aspects of the stream (e.g. headwaters and lower reaches) and as known locations of black fly larvae. Site 1 is on one of the headwaters of Sixmile Creek where the stream is less than 1 m wide, temporary, and running through an open marshy meadow. Site 2 (Hurd Road Stream) is a small stream in a forested area, typical of many small branches of Sixmile Creek. This particular branch enters a swamp which feeds

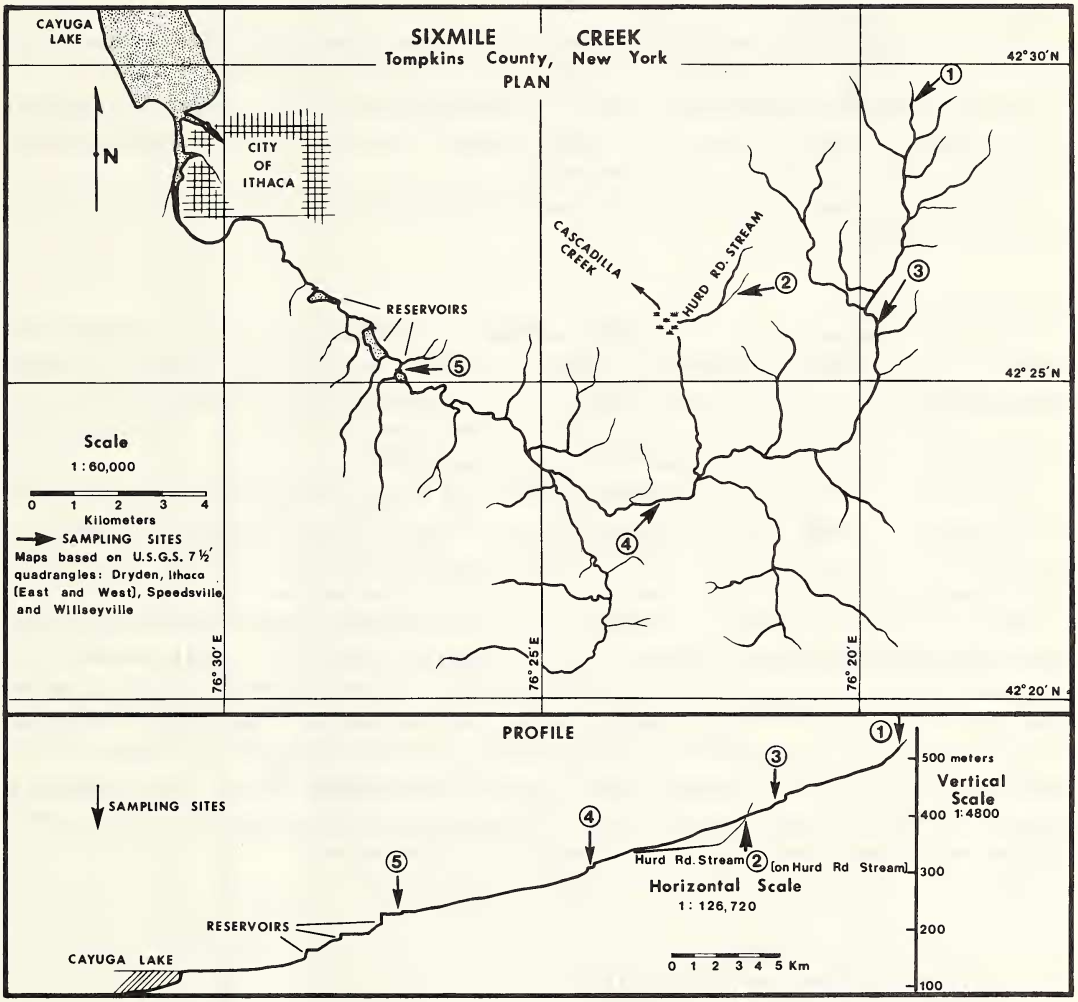

Figure 1. Sixmile Creek, Tompkins County, New York, USA. (Plan above and profile below) showing collecting sites: 1 = Sixmile Creek Headwaters (open headwater stream), 2 = Hurd Road Stream (forested headwater stream), 3 = Sixmile Creek at Sixhundred Road (forested lower reach), 4 = Sixmile Creek at Brooktondale (open lower reach), 5 = Sixmile Creek at Burns Road (dam spillway).

both Sixmile Creek and Cascadilla Creek. At Site 3, Sixmile Creek (at Sixhundred Road) has become large and permanent and flows in a rocky gorge through hilly, forested land. At Site 4 (at Brooktondale), the stream is in a shallow gorge, surrounded by farm land. Between Sites 3 and 4, there are long reaches of stream with fine-textured substrates (sand and fine gravel) which support a few larvae. A few samples were also taken at Site 5 (at Burns Road) where the stream passes over a dam spillway before entering a long gorge with forested sides. Detailed descriptions of these collection sites are given in Kurtak (1973).

Sites were visited monthly, or at least once in each of the four seasons in 1970 and 1971, and some again in 1972. Samples were taken during the daylight hours, but not at specific times.

Samples from different parts of the watershed were usually taken within a few days of each other, but not commonly on the same day, due to lack of time. If rainfall occurred in the interval between samples, a significant change in suspended material was possible.

In one instance, a special effort was made to sample the sites in a rapid sequence. Sites 1, 3, 4 and 5 were visited within a few hours.

Sampling procedure

Environmental parameters were measured at each site. These included surface velocity (measured by timing a float passing along a calibrated cord held in the current); temperature (measured to the nearest degree centigrade with an alcohol thermometer); and pH (measured with a Helige comparator using bromophenol red indicator). Notes were taken on the dimensions of the streams , the nature of the substrate, bank vegetation, and any other factors that seemed relevant.

Characteristics of the sites are summarized in Table 1 and 2. Two significant trends down the stream were increases in velocity and water temperature (in summer). Also, pH increased downstream in general, but decreased again at Site 5. Site 4 was densely populated in summer with up to 50 larvae/cm^2 of *Simulium pictipes*. Note that Sites 1 and 2 were both dry in the summer and early fall.

Black fly larvae were collected and returned to the laboratory alive for identification and dissection. They were identified according to Peterson (1970), Pinkovsky (1970), Stone (1964), and Stone and Jamnback (1955). Voucher specimens have been deposited in the Cornell University Insect Collection, Ithaca, New York (Lot. No. 1038). Whenever possible, identifications were made before removing the gut; otherwise, specimens were determined on the basis of preserved head capsules and skins. At least three individuals of each major species found at each site were selected and their guts removed and smeared on individual slides in Hoyer's medium. The composition of the gut content was determined in the same way as composition of samples of suspended material (see below).

The majority of the larvae collected were of the following species:

Cnephia mutata (Malloch)
Prosimulium fontanum Syme and Davies
Prosimulium fuscum Syme and Davies
Prosimulium magnum Dyar and Shannon
Simulium decorum Walker
Simulium parnassum Malloch
Simulium pictipes Hagen
Simulium tuberosum (Lunström)
Simulium venustum Say
Simulium verecundum Stone and Jamnback (species complex)
Simulium vittatum Zetterstedt

Table 1. Characteristics of stream sites. All sites are in Tompkins County, New York, USA.

Stream Site	Elevation (m)	Depth (m)[1]		Width (m)[1]		Velocity (m/sec)[2]		Average pH	Temperature °C (seasonal range)
		Low Flow	High Flow	Low Flow	High Flow	Low Flow	High Flow		
No. 1 (Sixmile Creek headwaters)	520	dry	0.15	dry	0.5	dry	1.0	6.8	3 – 14
No. 2 (Hurd Road stream)	365	dry	0.10	dry	1.7	dry	1.0	7.2	0 – 16
No. 3 (Sixmile Creek at Sixhundred Road)	395	0.04	0.15	5.0	7.0	0.7	1.8	7.2	0 – 18
No. 4 (Sixmile Creek at Brooktondale)	290	0.05	0.60	10.0	12.0	0.9	1.2	7.6	0 – 24
No. 5 (Sixmile Creek at Burns Road)	215	0.02	0.40	15.0	15.0	0.6	1.8	7.8	0 – 26

[1] Average dimensions through a 10-m reach.
[2] Surface velocity.

Seven liters of water were collected at each site for analysis of suspended material. The sample was dipped out as close as possible to the attachment sites of larvae when present, taking care not to stir up the substrate. Samples were stored at 4 C and usually processed within two days. They were centrifuged in a Foerst ® continuous centrifuge, permitting removal of 98% of the plankton-sized material and 25–50% of the bacteria (Welch, 1948). The centrifugate was subsampled by scraping the wall of the centrifuge bowl in several vertical bands with a 4 mm wide blade. Each subsample (two per water sample) was then spread thinly on a slide in a drop of Hoyer's medium. These slides were observed at a magnification of 300 diameters using a phase contrast microscope. At least five fields laid out in an "X" pattern were observed on each slide. Areas where particles were not in a single layer were avoided. Within each field, a 50 μm x 300 μm strip was divided into 12.5 μm x 12.5 μm squares using an ocular grid. Each of these units was examined and the category of particle which filled or dominated (>50%) it was determined.

Table 2. Additional characteristics of stream sites.

Site	Type of Terrain	Substrate	Permanence	Main black fly species present
No. 1	marshy meadow	stones, trailing grass	dry July-Oct.	*Cnephia mutata, Prosimulium fontanum, Simulium decorum, S. verecundum*
No. 2	wooded	0.1–0.3 m stones	dry Aug.-Oct.	*Prosimulium magnum*
No. 3	wooded	horizontal shale	permanent	*Prosimulium fuscum, Simulium parnassum, S. tuberosum, S. verecundum*
No. 4	wooded and cropland	horizontal shale	permanent	*Simulium pictipes*
No. 5	wooded and cropland	dam spillway	permanent	*Simulium vittatum*

Particles were classified as (1) mineral fragments (identifiable by their sharp-fractured edges and including fine sand, very fine sand, and silt[3], (2) organic fragments (mainly pieces of plant tissue), (3) diatoms and other algae, and (4) "fine material" less than 5 μm in diameter whose nature was undeterminable (including particles the size of fine silt and clay[3]). Polarized light was sometimes used to identify mineral grains by their crystalline nature. Other categories, such as filamentous algae, were employed as needed. No effort was made to count fungi, bacteria, or colloid particles. The size range of the particles was not determined in detail.

In the examination process, empty squares were not counted. Areas of large irregular particles were estimated as though the particles were smoothed to rectilinear shapes. Groups of particles less than 12.5 μm in length were assumed to be crowded together so that the space between them was negligible. Then the area (number of squares) occupied by the group was estimated. Finally, the percentage of each category in relation to the total number of squares counted was calculated for the five fields, and the mean of the two subsamples was determined. This permitted estimates of the composition of the samples on basis of area occupied by various types of particles in a thin smear.

[3]See United States Department of Agriculture (1951) for definitions of the sizes of soil particles.

The remaining 95% of the centrifugate was transferred to an aluminum weighing dish and dried at 60 C for 24 hours. The residue was then weighed to the nearest 0.01 mg to determine mg/l total suspended material.

Selected samples were also analyzed for oxidizable organic matter by the micro method of Maciolek (1962).

Digestion of diatoms

Although this study did not concern itself with what portion of the ingested suspended material was actually digested, a simple experiment was conducted with diatoms. Fresh, living diatoms (*Cymbella* sp.) were fed larvae of *Simulium jenningsi*, *Simulium pictipes* and *Simulium tuberosum* in the laboratory. The larvae were given no additional food, so the diatoms were retained for several hours. Every five minutes for the first 30 minutes after ingestion and at one-hour intervals for several hours thereafter, a sample of the larvae was taken. The guts were immediately removed and squashed on a slide and observed by phase contrast microscopy.

RESULTS

Suspended material and gut contents

The data from the stream water samples and gut-content analyses are presented in Tables 3 – 7. In these tables, each value for "water" represents the mean for 1–10 samples taken at that site in that month during the three years of the study. Each "gut content" value represents a mean for at least three larvae of each of the main species present when the water was sampled. The data for different species were combined if there were no significant differences among them. Coefficients of variation for groups of subsamples of a given water sample and groups of larvae collected at the same time were 10–20%. The stream stage (percent of the highest level of flow observed) and water temperature are also shown in the tables.

The dry weights of suspended material normally ranged from 1–13 mg/l (x = 4.6 mg/l). During flash flood periods, however, large amounts of silt and coarser mineral particles briefly raised the weights to several hundred mg/l. Such samples are not included in the means.

Usually at least 50% of the suspended material was mineral fragments or material less than 5 μm in diameter. This largely inorganic portion (see "Organic Content" below) accounted for most of the increase in total suspended material during high water periods (e.g. during March at Site 4, Table 6). The organic portion consisted largely of plant fragments and diatoms. *Fragilaria*, *Meridion*, *Gomphonema*, and *Cymbella* were the main diatom genera seen. Visible diatom coverings on the rocks in the streams tended to be more common in the late spring and early fall than in summer or winter.

In addition to the types of materials indicated in the tables, other materials were found occasionally in the gut contents. These included fragments of filamentous algae, aquatic mites, and fragments from other arthropods, including black fly larvae. Pollen, probably of *Pinus strobus* L., was important at Site 2 on one occasion, in both guts and water.

In terms of size, mineral particles generally ranged from 5–50 μm, diatoms from 20–100 μm, and organic particles varied from five to several hundred μm in diameter. Particles larger than 300–400 μm were rarely seen in the guts. Particles less than 5 μm, not separated as to type, often made up a large portion of the samples.

Proportions of various components of suspended material varied greatly with time and place. Water in upper reaches (Sites 1–3) contained fewer diatoms than that from lower reaches (Site 4). This trend is also clear from samples taken on one day (Table 7). The forested headwater stream at Site 2 contained

Table 3. Suspended material in water compared with the gut contents of black fly larvae at Site 1 (Sixmile Creek headwaters – open headwaters stream), 1970 – 1972. Predominant species: *Cnephia mutata*, *Prosimulium fontanum*, *Simulium decorum*, and *Simulium verecundum*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Contents of Suspended Material and Gut contents (estimated microscopically): Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles < 5 μm	Others
January (n=1)	3 C	33%	1.7	Water	18%	18%	42%	22%	0%
				Gut contents (*C. mutata*)	64%	6%	14%	16%	0%
				Gut contents (*P. fontanum*)	8%	23%	12%	57%	0%
February				NO DATA					
March (n=1)	3 C	53%	5.6	Water	5%	16%	23%	56%	0%
				Gut contents (all species)	23%	10%	4%	63%	0%
April (n=2)	9 C	100%	1.8	Water	17%	31%	20%	32%	0%
				Gut contents (all species)	22%	18%	6%	54%	0%
May (n=1)	NO DATA	NO DATA	1.8	Water	21%	18%	27%	54%	0%
				Gut contents (all species)	14%	12%	6%	68%	0%
June (n=3)	14 C	40%	1.8	Water	21%	16%	9%	54%	0%
				Gut contents (all species)	27%	14%	4%	55%	0%
July-Oct.				STREAM DRY					
Nov.-Dec.				NO DATA					

n= Number of times visited

Table 4. Suspended material in water compared with the gut contents of black fly larvae at Site 2 (Hurd Road stream – forested headwaters stream), 1970 –1972. Predominant species: *Prosimulium magnum.*

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Sample	Contents of Suspended Material and Gut Contents (estimated microscopically)				
					Diatoms	Mineral Fragments	Organic Fragments	Particles <5 μm	Others Others
January (n=2)	0 C	68%	3.0	Water	18%	22%	9%	51%	0%
				Gut contents	14%	25%	26%	35%	0%
Feb.-March	NO DATA								
April (n=2)	4 C	100%	8.0	Water	0%	7%	10%	83%	0%
				Gut contents	6%	18%	23%	53%	0%
May (n=2)	10 C	82%	2.4	Water	2%	9%	7%	82%	0%
				Gut contents	5%	22%	18%	55%	0%
June (n=1)	11 C	9%	NO DATA	Water	NO DATA				
				Gut contents	0%	16%	19%	65%	0%
July-Oct.	STREAM DRY								
November (n=1)	9 C	91%	2.0	Water	3%	15%	61%[1]	21%	0%
				Gut contents	25%	19%	13%[1]	43%	0%
December (n=1)	4%	82%	4.0	Water	0%	25%	28%	47%	0%
				Gut contents	NO LARVAE PRESENT				

n= Number of times visited

[1]Large fragments of leaves

Table 5. Suspended material in water compared with the gut contents of black fly larvae at Site 3 (Sixhundred Road – forested lower reach), 1970–1972. Predominant species: *Prosimulium fuscum*, *Simulium parnassum*, *Simulium tuberosum* and *Simulium verecundum*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Sample	Contents of Suspended Material and Gut Contents (estimated microscopically): Diatoms	Mineral Fragments	Organic Fragments	Particles < 5 μm	Others
January (n=1)	1 C	frozen	4.7	Water	5%	26%	15%	54%	0%
				Gut contents (all species)	NO LARVAE PRESENT				
February	NO DATA								
March (n=1)	0 C	100%	7.1	Water	0%	10%	41%	40%	0%
				Gut contents (all species)	18%	18%	11%	53%	0%
April (n=3)	8 C	80%	1.9	Water	17%	16%	23%	44%	0%
				Gut contents (all species)	11%	9%	18%	53%	0%
May (n=1)	15 C	47%	13.3	Water	1%	6%	10%	83%	0%
				Gut contents (all species)	7%	15%	21%	57%	0%
June (n=5)	15 C	33%	5.5	water	6%	23%	17%	64%	0%
				Gut contents (all species)	4%	16%	13%	67%	0%
July (n=1)	18 C	NO DATA	NO DATA	Water	NO DATA				
				Gut contents (all species)	21%	17%	18%	44%	0%
August	NO DATA								
September (n=2)	11 C	20%	2.0	Water	5%	25%	21%	48%	1%[1]
				Gut contents (all species)	13%	21%	10%	44%	2%[1]
October	NO DATA								
November (n=1)	2 C	7%	1.0	Water	0%	40%	32%	28%	0%
				Gut contents (all species)	NO LARVAE PRESENT				
December	NO DATA								

n= Number of times visited
[1] Pollen

Table 6. Suspended material in water compared with the gut contents of black fly larvae at Site 4 (Brooktondale – open lower reach), 1970–1972. Predominant species: *Simulium pictipes*.

Month	Water Temperature °C	Stream Stage (% of highest flow observed)	Total Suspended Material (dry wt. in mg/l)	Sample	Contents of Suspended Material and Gut Contents (estimated microscopically): Diatoms	Mineral Fragments	Organic Fragments	Particles <5 μm	Others
January	1 C	48%	4.0	Water	1%	12%	7%	80%	0%
(n=3)				Gut contents	5%	17%	10%	68%	0%
February	0 C	NO DATA	5.4	Water	0%	10%	4%	86%	0%
(n=1)				Gut contents	----------	NO LARVAE PRESENT		----------	
March	0 C	53%	12.9	Water	1%	18%	13%	68%	0%
(n=3)				Gut contents	11%	32%	12%	45%	0%
April	9 C	67%	3.5	Water	19%	16%	8%	67%	0%
(n=4)				Gut contents	20%	14%	8%	49%	0%
May	13 C	68%	2.0	Water	1%	16%	10%	63%	0%
(n=3)				Gut contents	2%	17%	4%	77%	0%
June	16 C	31%	8.0	Water	32%	16%	9%	43%	0%
(n=5)				Gut contents	48%	14%	4%	34%	0%
July	17 C	24%	3.3	Water	12%	10%	7%	61%	0%
(n=10)				Gut contents	16%	14%	8%	62%	0%
August	15 C	20%	4.2	Water	56%	18%	9%	17%	0%
(n=2)				Gut contents	54%	6%	14%	26%	0%
September	16 C	38%	4.1	Water	20%	25%	8%	47%	0%
(n=7)				Gut contents	30%	22%	8%	40%	0%
October	15 C	13%	1.4	Water	39%	19%	8%	34%	0%
(n=6)				Gut contents	36%	16%	7%	41%	0%
November	7 C	37%	12.6	Water	36%	16%	2%	46%	0%
(n=3)				Gut contents	30%	12%	11%	47%	0%
Deeember	4 C	93%	7.0	Water	30%	17%	6%	47%	0%
(n=1)				Gut contents	----------	NO LARVAE PRESENT		----------	

n= Number of times visited

Table 7. Suspended material in water compared with the gut contents of black fly larvae along the length of Sixmile Creek on June 7, 1971. Predominant species as indicated.

Site	Total Suspended Material (dry wt. in mg/l)	Water Temperature °C	pH	Estimated Discharge (m^3/sec)	Composition of Suspended Material and Gut Contents (estimated microscopically)				
					Sample	Diatoms	Mineral Fragments	Organic Fragments	Particles $<5\ \mu m$
No. 1 (Sixmile Cr. Headwaters–0.3 km from source)	5.6	14 C	6.8	0.005	Water	10%	33%	18%	39%
					Gut contents (*Simulium verecundum*)	6%	16%	4%	74%
No. 3 (Sixhundred Rd. –6.0 km from source)	2.1	15 C	7.6	0.39	Water	25%	25%	13%	37%
					Gut contents (*Simulium parnassum*)	27%	19%	8%	46%
No. 4. (Brooktondale–13.6 km from source)	3.5	20 C	8.0	0.7	Water	31%	34%	9%	26%
					Gut contents (*Simulium pictipes*)	77%	11%	4%	8%
No. 5 (Burns Road – 17.9 km from source)	3.8	21 C	---- NO DATA	------	Water	68%[1]	6%	3%	23%

[1] Mainly empty frustules

more organic particles and fewer diatoms at Site 3 than at Site 4, even though the substrates were very similar. In general, the lower reaches had more total suspended material.

Maximum quantities of suspended material occurred in spring and consisted mainly of mineral fragments or material less than 5 μm. In summer and fall, diatoms made up a large portion of total suspended material in the lower reaches, sometimes up to 50% (e.g. November at Site 4). Plant fragments were numerous at forested headwater site (Site 2) in fall, and at Site 3 in spring.

Proportions of material in guts tended to correspond to proportions of materials carried in the stream, except that larvae commonly contained a higher percentage of diatoms. Usually, gut contents of different species at the same site were quite similar. At Site 1 in January, however, there was considerable difference between those of *Cnephia mutata* and *Prosimulium fontanum*.

Differences between the years were not analyzed, since duration of this study was short.

Organic content of the suspended material

Results of the analyses for organic content are shown in Table 8. Total organic content varied from 0.35–1.11 mg/l (7.9–24%). The highest percentage of organic matter in the suspended material did not coincide with the highest total amount of organic matter per liter.

The highest percentages of organic matter were found where organic fragments were common (e.g. Site 2 XI-4-70). Unfortunately, none of the water samples from Sixmile Creek chosen for analysis had a high proportion of diatoms. To show that large quantities of diatoms also increased the organic content, a result from a site similar to Site 4 (Taughannock Creek) is also shown. Low percentages were associated with large proportions of mineral fragments and/or material less than 5 μm (e.g. Site 2 IV-6-71, Site 3 I-26-71, Site 4 I-26-71, and II-25-71).

Digestion of diatoms

Diatoms examined 15 and 30 minutes after ingestion showed no visible change in appearance other than loss of mobility. After 40–60 minutes, the diatoms began to lose their golden-yellow color and became more transparent, revealing the striations on the frustules and the internal organelles. The clearing occurred first in diatoms near the gut wall. Within 3.5 hours, frustules became completely clear. This is of course much longer than the usual retention time (see Discussion). Non-ingested fresh diatoms which were killed in hot water and stored at room temperature did not clear for a least 48 hours. The clearing occurred at similar rates for *Cymbella* sp. in guts of larval *Simulium pictipes*, *Simulium tuberosum* and *Simulium jenningsi*.

DISCUSSION

Reliability of data

Reliability of data gathered for this work is limited by the method of estimating proportions of various materials in samples. Applied consistently, estimation of composition by area should give good comparative information. However, for absolute measurement of suspended material, estimation by microscopical measurement of area is less accurate than volumetric measurement or direct chemical analyses, but is more accurate than counting (Sladeckova, 1962). Neither area or volume estimates allow for differences in density. In Table 8, there is only a general agreement between the microscopical and chemical analyses.

Also, the particulate material examined was only a small fraction of the total material collected in water samples, which in turn were a very small percentage of flow of the stream at a particular time. Another aspect of the sampling problem was daily variability in stream discharge and concurrent

Table 8. Analysis of the organic content of material suspended in streams, Tompkins County, New York, 1970–1971.

Stream Site		Date	Composition of Suspended Material (estimated microscopically)				Total Suspended Material	Organic Content[1]	
			Diatoms	Mineral Fragments	Organic Fragments	Particles < 5 μm	(mg/l)	(mg/l)	(% dry wt.)
No. 2	(Hurd Rd. Stream)	XI–04–70	3%	15%	61%	21%	2.01	0.48	24%
		IV–06–71	3%	21%	39%	37%	4.60	0.44	9.7%
No. 3	(Sixmile Creek at Sixhundred Road)	1–26–71	5%	27%	15%	53%	4.73	0.41	8.7%
No. 4	(Sixmile Creek at Brooktondale)	1–26–71	1%	21%	12%	66%	7.34	0.70	9.6%
		11–25–71	3%	49%	21%	29%	14.02	1.11	7.9%
	Taughannock Creek at Rabbit Run, 4.4 km below Waterburg, Romp Tomkins Co., N.Y.	VIII–25–70	60%	13%	6%	18%	2.52	0.35	14%

[1] Micro method of Maciolek (1962). One replication per sample. When three replications were made with another sample, the coefficient of variation was 12%.

variability in content of suspended material. Sampling was done in periods of stable base flow when possible. Another approach would be to use automatic equipment capable of continuous sampling.

Interpretation of the stream samples

Factors such as type of terrain in the watershed, the nature of the substrate, degree of shading by streamside vegetation, and water depth and velocity can be used to explain the observed temporal and spatial variations in the quantity and composition of suspended material in the stream, as well as distribution of black fly larvae.

In forested headwater streams such as Site 2, fallen leaves are the main part of the organic material. Coarse leaf fragments (>300 μm) are especially important in the fall. These streams provide practically no diatoms because of heavy shading. In open headwater streams, such as Site 1 (which is on a south-facing slope), diatoms grew abundantly on trailing grass even in January. Both types of headwaters can produce large numbers of larvae, but of different species (i.e. *Prosimulium magnum* at Site 2; *Prosimulium fontanum*, *Cnephia mutata*, and several *Simulium* spp. at Site 1).

Changes seen at downstream sites in this study can be explained by a description of changes along a stream similar to that shown by Cummins (1977). The material from headwater streams is comminuted and diluted as it is carried downstream. Additional organic particles enter the stream from the vegetation bordering the stream, but this contribution becomes less important in relation to the volume of the stream as it coalesces and increases in discharge. Diatoms and other algae washed off of the substrate contribute more to organic content at this stage. Amount of algal growth varies with suitability of substrate and amount of sunlight. Sand and silt are continuously eroded from banks. Higher water velocities downstream tend to keep more material suspended.

Consistent with this picture of downstream changes, diatoms were more important at Site 3 and at Site 2, but organic particles still made up over 50% of the organic fraction. The large (>300 μm) leaf fragments common at Site 2 were not seen at Site 3. The bedrock substrate at Site 3 would certainly be suitable for algal growth, but diatoms may have been limited by shade from the forested banks. At Site 4, the substrate was bedrock, but was exposed to the sun with only a thin layer of water flowing over it. The suspended material there exceeded 10 mg/l and was often nearly 50% diatoms, especially during later summer months when discharge was low, illumination high, and floodwaters did not frequently scour the streambed. In early spring, with high water, more silt was present.

The data taken all on the same day (Table 7) support the idea of a trend toward fewer large particles and more diatoms downstream. Below Site 4, however, the diatoms were mostly empty frustules.

The presence of diatoms and organic particles increases the percentage of organic matter, but does not necessarily increase the total amount per liter. However, a small amount of organic matter in a pure form may be more beneficial than a larger amount heavily diluted with silt.

Interpretation of the gut contents

Proportions of materials in gut contents generally reflected proportions in the water, with little difference among larvae of different black fly species present at a given site. This indicates that feeding is indiscriminate. It was not uncommon, however, to find larvae that contained a higher proportion of diatoms than that found in the associated water. In the case of *Simulium pictipes* (Site 4 in April), this could be the result of more efficient feeding on the diatoms, which are larger than the silt particles (Kurtak, 1978). Also other fractions of gut contents may be digested, leaving behind only the insoluble diatom frustules and falsely inflating the percentage of diatoms.

At Site 1 in January, larvae of *Cnephia mutata* contained a much larger proportion of diatoms than did the water or larvae of *Prosimulium fontanum* at the same location. This can be explained by the observation that larvae of *Cnephia mutata* often spend considerable time scraping material from the substrate rather than filter feeding (Kurtak, 1973).

No attempt was made to determine which components of gut contents are important in nutrition of black fly larvae, except to show that diatoms are in fact digested. The use of radioactive tracers would be one way to determine what portions of the gut content are assimilated.

It is clear that diatoms can be at least partly digested in the normal retention time, which is about one hour (Kurtak, 1978). Diatoms from larvae collected in natural habitats always appeared dead and clear since the larvae were held alive several hours before dissection.

Black fly larvae are known to ingest bacteria (Snoddy and Chipley, 1971) and there is evidence that bacteria may be an important food source in large rivers (Fredeen, 1960,1964). No bacteria could be found in Sixmile Creek, but coliform bacteria are certainly present where the stream banks are densely populated. Truly rheophilic bacteria may also be present. These, however, are usually few in number and are difficult to culture (Hynes, 1970). Considerable numbers of bacteria may be associated with decomposing plant fragments in the water.

Black fly larvae also reportedly ingest particles as small as colloids (Wotton, 1976), but these particles require electron microscopical techniques to detect.

From the data it appears that the choice of a specific habitat by a black fly species has a strong influence on what kind of food the larvae will be exposed to. Larvae of *Simulium pictipes*, for example, which were characteristically found on bedrock substrates near waterfalls, usually contained large numbers of diatoms. The larvae of *Prosimulium magnum* on the other hand, usually contained large amounts of leaf fragments obtained in the small, shaded, forest streams where they lived. Another instance of direct relationship between habitat and food is reported by Carlsson *et al.*, (1977), who reported that larvae occurring below a lake in Sweden received nutrients in the form of fine particulate organic matter from the lake bottom. In the region of the present study, however, there were other species which occurred in a very wide range of habitats, such as *Simulium tuberosum* which Pinkovsky (1970) found at 85% of the sites he sampled in Tomkins County. Larvae of such a species would be exposed to a wide range of food.

ACKNOWLEDGEMENTS

Thanks are due to Dr. B.V. Travis, Dr. C.O. Berg, and Dr. J.M. Kingsbury of Cornell University who served as the author's Ph.D. thesis committee and guided this study.

This research was supported in part by a National Science Foundation Fellowship and by a Cornell Fellowship. Further support came from Hatch Act funds and a grant from the Grace Griswold Fund of the Cornell Department of Entomology helped to defray publication costs.

Dr. Gary R. Mullen of Auburn University and Dr. Richard W. Merritt of Michigan State University read the manuscript and made valuable suggestions.

REFERENCES

Anderson, J.R. and R.J. Dicke. 1960. Ecology of the immature stages of some Wisconsin black flies. Annals of the Entomological Society of America 53: 386–404.

Burton, G.J. 1973. Feeding of *Simulium hargreavesi* Gibbons larvae on *Oedegonium* filaments in Ghana. Journal of Medical Entomology 10: 101–106.

Carlsson, M., L.M. Nilssen, B.J. Svensson, S. Ulfstrund and R.S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simulium) inhabiting lake outlets in Swedish Lapland. Oikos 29: 229–238.

Chance, Mary M. 1970. The functional morphology of the mouthparts of black fly larvae (Diptera: Simuliidae). *Quaestiones Entomologicae* 6: 245–284.

Cummins, K.W. 1977. From headwater streams to rivers. American Biology Teacher 39: 305–312.

Davies, D.M. and P.D. Syme. 1958. Three new Ontario black flies of the genus *Prosimulium*. Part II. Ecological observations and experiments. Canadian Entomologist 90: 744–759.

Emery, W.T. 1913. The morphology and biology of *Simulium vittatum* and its distribution in Kansas. Kansas University Science Bulletin 8: 323–362.

Fredeen, F.J.H. 1960. Bacteria as a source of food for blackfly larvae. Nature, London 187: 963.

Fredeen, F.J.H. 1964. Bacteria as food for black fly larvae (Diptera: Simuliidae) in laboratory cultures and natural streams. Canadian Journal of Zoology 42: 527–548.

Hynes, H.B.N. 1970. The ecology of running waters. University of Toronto Press, Toronto, 555 p.

Kurtak, D.C. 1973. Observations on filter feeding by the larvae of black flies (Diptera: Simuliidae). Ph.D. thesis. Cornell University, Ithaca, New york. 157 pp.

Kurtak, D.C. 1978 Efficiency of filter feeding of black fly larvae (Diptera: Simuliidae). Canadian Journal of Ecology 56: 1608–1623.

Maciolek, J.A. 1962. Limnological organic analyses by quantitative dichromate oxidation. Research Report of the United States Fish and Wildlife Service. No. 60.

Naumann, E. 1925. Notizen zur Ernahrungsbiologie der minischen Fauna. Arkiv fur Zoologie 16: 1–15.

Neeley, J.A. 1965. Soil survey of Tompkins County, New York. United States Department of Agriculture, Soil Conservation Service, Soil Survey Series 1961 No. 25.

Pacaud, A. 1942. Notes biologiques sur une station de *Simulium aureum* Fries aux environs de Paris. Bulletin Biologique de la France et la Belgique 76: 226–238.

Peterson, B.V. 1970. The *Prosimulium* of Canada and Alaska (Diptera: Simuliidae). Memoirs of the Entomological Society of Canada No. 69: 1–216.

Pinkovsky, D.D. 1970. An ecological survey of the black flies (Diptera: Simuliidae) of Tompkins County, New York. M.S. Thesis. Cornell University Ithaca, New York. 250 pp.

Puri, I.M. 1925. On the life-history and structure of the early stages of Simuliidae. Part I. Parasitology 17: 295–369.

Sladeckova, A. 1962. Limnological investigation methods for the periphyton ("Aufwuchs") community. Botanical Review 28: 286–350.

Snoddy, E.L. and J.R. Chipley 1971. Bacteria from the intestinal tract of *Simulium underhilli* (Diptera: Simuliidae) as a possible index to water pollution. Annals of the Entomological Society of America 64: 1467–1468.

Stone, A. 1964. Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. Fascicle 9. Simuliidae and Thaumaleidae.Bulletin of the Connecticut State Geological and Natural History Survey No. 97.

Stone, A., and H.A. Jamnback. 1955. The black flies of New York State (Diptera: Simuliidae). Bulletin of the New York State Museum No. 349: 1–144.

United States Department of Agriculture. 1951. Soil Survey Manual (United States Department of Agriculture Handbook No. 18) United States Government Printing Office, Washington, D.C. 503 pp.

United States Geological Survey. 1967. Water resources data for New York (1965). Part 1. Surface water records. Water Resources Division of the United States Geological Survey, Albany, New York. 490 pp.

Welch, P.S. 1948. Limnological methods. McGraw-Hill Book Company, New York, 381 pp.
Williams, T.R. 1961. Size of particles ingested by *Simulium* larvae. Nature, London. 189: 78.
Wotton, R.S. 1976. Evidence that black fly larvae can feed on particles of colloidal size. Nature, London 261(5562): 697.
Wotton, R.S. 1977. The size of particles ingested by moorland stream blackfly larvae (Simuliidae). Oikos 29: 332–335.